

Cycling and status of boron in two forest types in Greece

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Abstract: The status and cycling of boron (B) were examined in two forest types in Greece, a maquis and a mountainous fir forest. In the hydrological cycle, in both forest types, the B concentration in the bulk deposition was significantly lower than that in throughfall implying dry deposition. It was also shown that some long-range transfer of B took place in the atmosphere above both forests. The total B in soils was higher in the maquis forest reflecting the chemical composition of the parent material but also the proximity of the maquis forest to the sea. Likewise, the B concentration in the holm oak leaves in the maquis forest was higher than that in the fir needles. These facts affected the B concentrations in the soil solution and fluxes in the hydrological cycle and litterfall of both forests. In soils, the available B correlated significantly with the organic carbon and the ratio of C/N in both forests but not with the total B. The residence time of B in the forest floor was lower in the maquis plot, which means faster cycling. The low temperatures in the mountain fir plot contributed to this fact.

Keywords: amaquis, fir, boron, hydrology, soil, cycling.

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Introduction

Boron (B) is an essential micronutrient for the growth of all plants. It plays a key role in a variety of plant functions including cell division and sugar translocation. It is also required for the production of nucleic acids and the development of reproductive structures (Nazir et al. 2016, Kabu & Acosman 2013). The current understanding of the biological function of B in plants is that it

plays a structural role in both the cell wall and plasma membrane (Wang et al. 2015).

Boron (B) is found in several minerals hydrous borates, anhydrous borates and complex borosilicate (Evans & Sparks 1983). The product of weathering of these minerals brings B into solution mainly as boric acid (H_3BO_3). The latter is the main form of B taken up by plants and the second is the borate anion (Hu et al. 1997, Kumar & Purkait 2020). In addition, the uptake

of organic complexes with B can also take place.

In agricultural plants, the range between B deficiency and B toxicity is very small (Choi et al. 2015). It is so small that deficiency and toxicity thresholds can alternate due to mild environmental changes (Kumar et al. 2022). Boron toxicity is a severe problem in many parts of the world, but mainly in arid regions not dominated by trees. It was found that after fertilization foliar B concentrations in conifers could increase from, for example, 1–2 mg·kg⁻¹ to over 100 mg·kg⁻¹ with no sign of toxicity. In contrast to toxicity, boron deficiency is a widespread problem in both agriculture and forestry, particularly on sandy and alkaline soils (Wang et al. 2015). The nature of the parent material is important. Soils developed on granite or basalt have low B concentration (Hingston 1986). Boron deficiency of forest trees occurs in many countries, mainly in plantations of eucalypts and pines, but also in plantations and natural stands of native species on soils altered by macronutrient fertilization, fire or erosion (Stone 1990). Boron deficiency is a major cause of loss in productivity in East Coast Australian radiata pine plantations (Turner et al. 2021). Lai et al. 2023 demonstrated that the B management in the tree nurseries of broad-leaved species is a key factor for obtaining high-quality seedlings, as optimum B supplementation helps improve their growth and nutrient uptake.

The aim of this work was to examine the cycles and status of B as well as the dependency of the available B in two forested plots, a maquis and a fir one. Both soils were derived from flysch, a sedimentary rock type. However, the fact that the plots are situated at different altitudes and have different vegetation makes their comparison worth studying.

Materials and Methods

Sites description

The two sites, from which the material was collected, belong to the Intensive Monitoring

Survey of the ICP Forests network (UN-ICP-FORESTS). The coordinates of the plots are Maquis: Latitude +38 50 46, Longitude +21 18 18, Fir: Latitude +38 52 28, Longitude +21 51 57. They stand for important forest ecosystems in Greece and this was the reason they were selected. The main forest vegetation for the first plot is maquis vegetation, consisting of Holm oak (*Quercus ilex* L.), strawberry trees (*Arbutus unedo* L.) and green olive trees (*Phyllirea latifolia* L.). The average age of the plants is 80-90 years. The soil is a clay loam one and is classified as Haplic Luvisol (WRB 2006). The pH (measured in water, ratio 1:5 soil to water) ranged from 6.1 to 6.6. The second plot is a Bulgarian fir (*Abies borisii-regis* Mattf.) stand with an approximate age of 100-110 years. The soil there is also a clay loam one; it is deep and classified as a Cambisol (WRB 2006). The average pH (also determined in water) of the FH horizon was 6.48 and that of the mineral layers ranged from 6.07 in the soil surface to 5.32 down to 80 cm depth. Information on the soil properties of both plots is shown in Table 4.

An important point, related to B availability, is that the maquis forest is close to the sea (15 km in contrast to the 250 km distance of the fir forest). Concise information is shown in Table 1. The average ambient temperature in the maquis plot was 15.1°C, whereas in the fir plot, it was 10.1°C (both temperature values including the rainfall heights in Table 1 were derived from 47 years of observations). A more detailed description of the plots is given by Michopoulos et al. (2021).

Table 1 Characteristics of the two forested plots.

Area	Plot altitude (m)	Soil parent material	Average annual rainfall (mm)	Main forest vegetation
Western Greece	360	Sandy flysch	1049	Holm oak, strawberry trees, green olive trees
Central Greece	1170	Argillaceous flysch	1449	Bulgarian Fir

Collection of samples from the hydrological cycle

Water samples analyzed for B were collected weekly from both plots. More specifically, samples from the throughfall deposition were collected weekly with 20 collectors placed randomly within the forested stands and bulk deposition with three collectors installed in a clearing at a distance of approximately 100 m from the plot centres. At the end of each month, the water samples formed a pooled sample. There were 26 measurements (representing 26 months) of throughfall and bulk deposition.

Soil solution samples were also collected weekly with zero tension lysimeters installed in two soil depths, 20 and 65 cm. Likewise, the soil solution samples formed a pooled sample at the end of each month. There were 22 measurements in the maquis plot and 17 measurements in the fir plot (representing 22 and 17 months for each plot, respectively).

The periods of water samples (bulk, throughfall, soil solution) collection for the two plots cover two hydrological years; i.e., October 2012 to October 2014. Michopoulos et al. (2022a) gave details of the collection of the water samples.

Collection of litterfall

In both plots, litterfall was collected with 10 plastic cylinders systematically placed in a straight line at fixed distances (5 m from each other). Each cylinder had a surface area of 0.242 m². A composite litterfall sample derived from the 10 traps was transferred to the laboratory after each sampling. In the laboratory, the litterfall was separated into its fractions, foliar, woody (twigs, bark parts) and rest (flowers, lichens, mosses, insect frass). All fractions were weighed after drying at 80°C for 2 days. Subsamples were ground in a ball mill for total analysis. The litterfall data (for B) covers the second hydrological year (2013-2014) for both plots.

Collection of needles and leaves

In both plots, needle and leaf samples were collected in 2017, 2019 and 2021 in winter (dormant period). The samples were collected from the upper one-third of the crown from five dominant trees and formed a pooled sample. From the maquis plot, the leaves were collected from the holm oak trees, which were the dominant species. The leaves collected were from the current and rest years. From the fir plot, it was the fir needle collected. Needles and leaves were dried at 80°C for 48 h and then ground in a special mill (for plant tissue grinding) and stored for analysis.

Collection of soil samples

Soil collection was carried out by systematic sampling in 2007. For each layer of the L, FH, 0–10 cm, 10–20 cm, 20–40 cm and 40–80 cm depths three replicates in space were formed. Details of the soil sampling can be found in Michopoulos et al. (2022a).

The L and FH layers were weighed. The bulk density of mineral soils in all layers was measured by a cylinder having a volume of 129 cm³. The samples of the FH and mineral layers passed through a 2 mm sieve and were stored for analysis.

Subsamples of the L, FH and mineral soils were pulverized in a ball mill for total elemental analysis.

Chemical analysis

The concentrations of B in water samples (bulk, throughfall and soil solution) were determined with an ICP-MS instrument (Thermo iCAP Qc).

Litterfall and foliage samples were digested in a mixture of HNO₃-HClO₄ and their B content was measured with the ICP-MS instrument mentioned above.

In the FH horizon and mineral soil layers the exchangeable Ca²⁺, Mg²⁺, K⁺, Al³⁺ and Mn²⁺ (the hydrogen ion concentrations were negligible) were extracted with a 0.1 M unbuffered

BaCl₂ solution and their concentrations were determined with the ICP-MS instrument. The Cation Exchange Capacity (CEC) was found by summing the concentrations of all the exchangeable cations. The concentrations of total N and organic C in soils were measured with a CN analyzer (Vario MAX). For the total B in soils, soil samples (including the L layer) were digested in a microwave oven with HF and aqua regia at a temperature range of 160–170°C for 20 min. Concentrations of B in the digests were determined with the ICP-MS instrument. The available B in soils was extracted with hot water and the azomethine-H reagent was used for the colour development to find the B concentration in the extracts (Jones 2001).

Calculations and statistical analysis

Hydrological cycle

There were statistical comparisons between the B concentrations in bulk and throughfall deposition for each plot. The Shapiro-Wilk test was applied to check the normality distribution. The fluxes of bulk and throughfall deposition were calculated based on B concentrations and precipitation volumes. In addition, the volume weighted-means of B for each hydrological year was calculated.

The concentrations of B in the soil solution in the 20 and 65 cm were compared statistically, i.e., for each depth the B content in one plot was compared with the B content in the other plot. Again, the Shapiro-Wilk test was applied to check for normality.

The effect of the earth's crust on the concentration of B in bulk deposition was assessed according to the following: The ratio value $(B_b / A_{lb}) / (B_c / A_{lc})$ stands for the degree of influence of the earth's crust on the composition of rain. In the equation, B_b is the concentration ($\mu\text{g}\cdot\text{L}^{-1}$) of B in bulk deposition, A_{lb} is the concentration ($\mu\text{g}\cdot\text{L}^{-1}$) of Al in bulk deposition; B_c is the concentration ($\mu\text{g}\cdot\text{g}^{-1}$) of B in the earth's crust and A_{lc} the concentration ($\mu\text{g}\cdot\text{g}^{-1}$) of Al also in the earth's crust. The higher the ratio, the higher the

impact has on the long-range transport of an element. Song and Gao (2009), Zhou et al. (2012), Michopoulos et al. (2022b) and others used this relationship to find the degree of contribution of the earth's crust to elemental concentrations in rain. The last mineral soil layer (40-80 cm) was considered to represent the content of B in the earth's crust for each plot. The average Al concentration of 8.8 % in the earth's crust taken from Kabata-Pendias and Pendias (2000) was used in the above equations.

The residence time of B in the forest floor was calculated by the Gosz et al. (1976) equation as the ratio $H/(L+\text{Thr})$ of the total pool of B in the forest floor over the incoming B fluxes (litterfall and throughfall) on the soil surface. The forest floor is formed by the L and FH horizons taken together as one layer.

Vegetation

The average concentrations and coefficient of variations for B in the holm oak and fir needles were calculated for the three years mentioned above. The litterfall fluxes were calculated for one year taking into account the litterfall concentrations of B and litterfall masses.

Soils

The soil properties, including total and available B in each plot, were compared with respective values of the same variables in the other plot through a paired t-test (for each soil layer) to find out if the dependency of available B would involve both plots (24 values) or not. If not, the statistics would be applied separately for each plot (12 values for each plot). The FH horizon would be excluded because they do not include all soil properties, clay for example. Again, the Shapiro-Wilk test was used to check for normality.

It was decided that the available B would be correlated with total B as well as with the organic C, the ratio of organic C/total N, the clay percentages, the cation exchange capacity (CEC) and soil pH in H₂O. The aim was to find

the dependency of the available B.

Results

Hydrological cycle

For the hydrological cycle, the statistics used were non-parametric, as the test for normality was negative. The volume-weighted means of B concentrations of the two hydrological years are shown in Table 2. The B concentration found in throughfall was significantly higher than that in the bulk deposition in both plots (Mann-Whitney test). The same happened in the fluxes of throughfall. The concentration of B in the soil solution at both depths was significantly higher in the maquis plot (Fig.1).

Table 2 Volume weighted means ($\mu\text{g}\cdot\text{L}^{-1}$), fluxes ($\text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) of bulk and throughfall in the hydrological cycle as well as enrichment factor (medians) in rain in the two forested plots in two hydrological years.

		Means			
		Maquis		Fir	
		Bulk	Throughfall	Bulk	Throughfall
1 year		4.04	14.7	2.56	5.23
2 year		3.91	14.0	4.28	7.78
		Fluxes			
		Maquis		Fir	
		Bulk	Throughfall	Bulk	Throughfall
1 year		79.5	124	60.6	93.4
2 year		84.4	125	76.2	111
		Medians of enrichment factors and ranges			
		Maquis		Fir	
		636 (12-2971)		465 (116-3027)	

Vegetation

The concentrations of B in leaves and needles are in Table 3. The coefficients of variations are rather high. There was not any statistical comparison as the number of observations is only three for both current and older tissues.

Soils

All variables passed the test of normality apart from the total B. The available B passed the test after carrying out a square root transformation. Accordingly, the statistics used

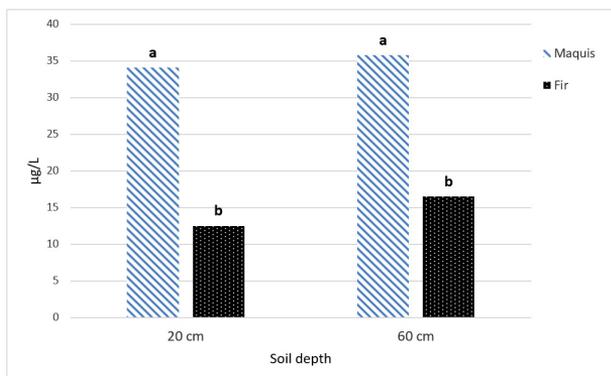


Figure 1 Concentrations of B in soil solutions in 20 and 60 cm depth in the two forest plots. Different letters in each depth stand for significant differences for at least 0.05-probability level

Table 3 Concentrations (mg kg^{-1}) of B in the standing leaves (current year and older) and litterfall fluxes of B ($\text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) in the two forested plots in the second year

Standing leaves concentrations		
	Maquis	Fir
Current year	16.0 (37)*	6.70 (24)
Older years	19.0 (44)	11.0 (45)
Litterfall fluxes in the second year		
	Maquis	Fir
Leaves	138	50.5
woody	8.52	2.93
Rest	3.13	5.24

Note: * Coefficient of variation (%)

were parametric. The paired t-test showed that total B, pH and CEC were found significantly higher in the maquis plot, whereas clay and organic C were found significantly higher in the fir plot. The concentrations of available B did not differ between the plots but as the other variable differed, the correlations were applied separately for each plot.

The percentages of available B defined as the percentage (%) of available B over the total B did not differ between the plots. However, the soil depth played a significant role as the percentage in both plots went lower with higher depths. In contrast, the total B went increasing with depth in both plots (Table 4).

Table 5 shows all the significant correlations that the total, available and percentage of available B had. Both the available B in absolute values and percentages had significant relations with organic matter and the ratios of C/N.

Table 6 shows the pools of B ($\text{kg}\cdot\text{ha}^{-1}$) in the forest floor and mineral soil, fluxes ($\text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) in litterfall and throughfall and residence time (years) of B in the forest floor of the two plots. It is striking that the pool of B in the mineral soil is hundreds of times larger than in the forest floor.

Table 4 Selected soil properties in the soil layers of the two forested stands. Clay and organic C are expressed in percentages (%), CEC in $\text{cmol}_c \text{kg}^{-1}$, total and available B in mg kg^{-1} .

Maquis						
Layer	pH	Clay	CEC	C	Total B	Available B
L				49.4 (2.8)	19.7 (48)	
FH	6.60 (3.7)*		71.6 (8.1)	26.0 (7.1)	32.4 (2.4)	2.47 (69)
0-10 cm	6.26 (2.0)	23.6 (6.2)	24.5 (12)	5.0 (14)	47.4 (6.0)	1.80 (29)
10-20 cm	6.18 (6.6)	24.2 (14)	15.8 (20)	2.73 (17)	48.9 (7.7)	0.94 (16)
20-40	6.12 (2.3)	26.0 (19)	12.8 (11)	1.44 (17)	50.4 (5.6)	0.95 (20)
40-80	6.53 (5.7)	29.3 (15)	13.7 (13)	0.86 (14)	94.9 (3.7)	0.34 (12)
Fir						
Layer	pH	Clay	CEC	C	Total B	Available B
L				50.8 (0.7)	5.68 (26)	
FH	6.48 (0.2)		57.8 (9.5)	23.0 (14)	19.8 (9.4)	5.44 (68)
0-10 cm	6.07 (2.0)	27.2 (2.0)	17.9 (15)	5.12 (20)	29.2 (8.2)	1.50 (37)
10-20 cm	5.77 (3.1)	31.2 (2.1)	10.9 (15)	3.36 (10)	31.1 (7.7)	0.75 (15)
20-40 cm	5.54 (1.2)	33.0 (6.7)	7.5 (7.9)	2.75 (3.5)	40.9 (6.6)	0.96 (42)
40-80 cm	5.32 (1.5)	34.9 (14)	3.8 (15)	1.53 (19)	37.4 (8.3)	0.55 (49)

Note:*Coefficient of variation (%)

Discussion

Hydrological cycle

In bulk deposition, the annual weighted means are not very different. However, the Mann-Whitney test showed that the monthly

Table 5 Significant Pearson correlation coefficients for available B (Av. B), total B (Tot. B) and percentage of B (Perc. B) and the rest properties in soils

Maquis					
	Org C	pH	Clay	C/N	Total B
Av. B	0.884	-	-	0.847	-0.760
Tot B	-0.620	-	0.596	-0.809	-
Perc. B	0.892	-	-	0.881	-
Fir					
	Org C	pH	Clay	C/N	Total B
Av. B	0.774	0.643	-0.559	0.707	-
Tot B	-0.703	-0.747	0.706	-0.687	-
Per B	0.855	0.738	-0.632	0.768	-

Table 6 Pools of B ($\text{kg}\cdot\text{ha}^{-1}$) in forest floor and mineral soil, fluxes ($\text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) in litterfall and throughfall and residence time (years) of B in the forest floor of the two plots.

Maquis			Fir		
Forest floor	1.20		1.63		
Mineral soil	230		172		
Litterfall	150		58.5		
Throughfall	125		102		
Residence time of B in the forest floor					
Maquis			Fir		
Years	4.3		10.2		

weighted means differed significantly in the bulk deposition. Park and Schlesinger (2002) quoted the medians of B concentrations in rain in several areas in the world. They found a value of $4.35 \mu\text{g}\cdot\text{L}^{-1}$ in continental sites and $6.60 \mu\text{g}\cdot\text{L}^{-1}$ in marine/coastal sites. In our work, the fluxes of bulk deposition ($60\text{-}84 \text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) were rather high compared to the existing data in northern European countries. Winker (1983) compiled data from research around the world about the fluxes of B in bulk deposition. The average value in Scandinavian countries was $30 \text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. In Germany, the range in B fluxes was $10\text{-}170 \text{g}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Very close to the annual fluxes in our work, were found by Boyed and Walley (1972) in the annual rainfall input of B in two Mississippi sites and one site in South Carolina the range of which was 62.7 to $74 \text{g}\cdot\text{ha}^{-1}$. The difference is probably due to the low content of B in igneous rocks (and

consequently in the soils derived from that parent material) that Scandinavian countries have in abundance.

There has been no publication on throughfall deposition. There was an appreciable enrichment in throughfall concerning the bulk deposition in both plots, especially in the maquis plot. This fact is probably due to the dry deposition of marine derived-aerosols in the maquis site, which is close to the sea. In areas with natural deposition from sea sprays, B originating from seawater is a major B input (Lehto et al. 2010). This kind of dry deposition of B is assumed to be the gas-phase concentration of B in the atmosphere, which is assumed to be boric acid vapour (H_3BO_3) (Anderson et al. 1994). This enrichment will play an important role in the shortening of the B residence time in the forest floor, as will be seen below.

Crustal enrichment in rain

The B enrichment had some values higher than 10 and lower than 500 (Table 2). In addition, the variability was found high as the ranges showed. This means that some anthropogenic influence related to the transfer of B in the atmosphere is probable. Poissant et al. (1994) argued that ratios in the range of 1 to 10 imply a large effect of the earth's crust on the composition of the elements in the rain, whereas values between 10 and 500 imply a rather moderate effect of the earth crust and the rest is complemented by anthropogenic influences. In our work, more than half of the crustal enrichment measurements (about 12 and 11 in the maquis and fir, respectively) were above 500. Therefore, the nutrient cycling due to the long-range transfer of B should not be underestimated.

Vegetation

In both species, the older leaves, holm oak and Bulgarian fir, had higher concentrations of B. This means that the process of retranslocation can cover some B demands if needed. Stone

(1990) compiled data from both broadleaves and conifers. For some *Quercus* species, the range of B deficiency was 14-16 $mg \cdot kg^{-1}$, whereas for most conifers the limit was 6 $mg \cdot kg^{-1}$. Winker (1983) argued that the concentration of B in one-year Sitka spruce trees decreased with diminishing maritime influence in Scandinavian forests. He found that in the inward country, the current year needles the B content was as low as 5 $mg \cdot kg^{-1}$. In our work, we are above these limits, especially for the older plant tissues. These ranges have to be considered with caution, as they are different species from the ones in this work. It is worth mentioning that the holm oak is an evergreen species and not a deciduous one like those mentioned in the list by Stone (1990). In addition, the foliar analysis serves as an indication for possible nutrient deficiencies but they have to be complemented with fertilization trials for verification.

The fluxes of B litterfall comprise only one year and we have to be careful with interpretations because the litterfall varies each year as it is affected by environmental factors. We suggest adding more data to B fluxes in the future to be more confident in this respect.

Soil

Soils developed on sedimentary rocks, like those in our case, have higher B concentrations than soils with other parent materials (Dasa & Purkai 2020). It would be expected that the concentration of total B would not be significantly different in the soils of the fir and maquis plots because of the same parent material. Moreover, the clay content was significantly higher in the fir plot, which is another reason against the result found. However, in our case, there is a serious exception. The maquis plot is close to the sea. High quantities of B are concentrated in marine evaporites and marine argillaceous sediments (Kabata-Pendias & Pendias 2000). It can be inferred that the proximity to the sea played a serious role in the higher content of total B in the maquis plot.

In the FH horizon, the concentrations of available B are considered high and in the first mineral layer (0-10 cm) sufficient for growth (Table 4). Below the limit of $1.0 \text{ mg}\cdot\text{kg}^{-1}$, the concentrations are insufficient and in the range of $1\text{-}2 \text{ mg}\cdot\text{kg}^{-1}$ sufficient for normal growth (Jones 2001). In terms of the available B percentage some authors claim that the available B constitutes 1-2% of total soil B (Jin et al. 1987, Tsalidas et al. 1994). In our work, we have higher percentages in the first soil layers. From Table 4 the calculated average percentages were for the FH layers 7.7% and 38.3% for the Maquis and fir plots, respectively. It can be concluded that the first layers are the most important in providing plants with B. The reservation is that the ranges for B sufficiency in soils were quoted for agricultural plants. Forests have developed systems to thrive in infertile soils. Boron has a high affinity for forming complexes with hydroxyl groups, such as organic acids (Dembitsky et al. 2002). The excretion of low molecular weight organic acids in the rhizosphere is something usual in forest soils. These acids can chelate Fe and Al from oxides and thus release B in soil solution. Therefore, plants can take up B from deeper layers. Still, these ranges can serve as a possible indication of B deficiency in forest soils.

The correlation of available B and the percentage of available B with the organic matter and the C/N ratios was something to be expected. Boron is related to soil organic matter, and availability will be affected by factors affecting organic matter mineralization such as dry conditions (Gupta 1967). The total B did not correlate with the available B. It was found to correlate with the clay content in the soil of both plots. In general, the total B is not a good predictor of available B (Nable et al. 1997). In a beech stand on calcareous soil, Roux et al. (2022) found that B cycling was much more important than the total B concentration. An explanation is that the B occluded in clay minerals is unavailable to plants. However, in our study, the percentage

of available B, in which the total B variable exists as the denominator in the ratio, was found to correlate significantly and positively with both the organic C and the ratio of C/N (Table 5). This means that the mineralization of organic matter contributed to soil weathering releasing B in the soil solution in both plots. In the fir plot, the soil pH had a positive significant relationship with the available B. The soil pH is an important factor affecting the availability of B in soils. Generally, the B bioavailability is lower when the pH of the soil solution is high. B adsorption by soils increases as the pH of the soil solution rises from 3 to 9 and it decreases when the pH increases further from pH 10 to 11.5 (Das & Purkait 2020, Saha et al. 2017). In the ranges of pH in the soils of both plots, the available B is in the form of H_3BO_3 , which is easily leached (Keren & Bingham 1985). The positive relationship of the pH with the available B should be attributed to other factors. It seems that the organic matter mineralization rates are the predominant factor in affecting the concentrations of available B in soils.

Soil solution

The pattern of B in soil solution followed that of total B in soils in both soil depths (Fig. 1). Boron can rapidly be leached down in soils (Gupta 1979) or it can be accumulated as evaporite deposits in arid climates (Evans & Sparks 1983). None of the forest plots in this work can be considered to have an arid climate. Weathering is more intense in the maquis plot bringing more B in the solution. As mentioned above, weathering is related to the organic matter mineralization. The latter was found more rapid in the maquis plot due to higher temperatures measured in soil layers (Michopoulos et al. 2021).

Residence time in the forest floor

We can see that the residence time of B in the forest floor of the maquis plot is shorter than that in the fir plot. This is because the incoming

fluxes of B in the maquis plot are higher than those in the fir plot. This in turn is owed to the higher concentrations of B in throughfall and litterfall. Although the forest floor contains far lower loads of B (Table 6), the forest floor is the most biologically active layer in soils and this is the reason why the residence time is essential knowledge.

Conclusions

The higher concentrations of B in soils and vegetation in the maquis plot affected the B content in soil solution and residence time in the forest floor.

The proximity to the sea played an important role.

The first soil layers were found important in providing plants with B.

In any case, the availability of B to plants depends on organic matter and its mineralization rates and not to total B in soils.

Conflict of interest

The authors declare there is no conflict of interest regarding the publishing of the paper, which does not include any form of plagiarism.

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